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ON

WHALES, PAST AND PRESENT,

AND

THEIR PROBABLE ORIGIN.

A DISCOURSE

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DELIVERED AT

THE ROYAL INSTITUTION,

FRIDAY, MAY 25, 1883.

Trans. to Mus. of Comp. Zool.

Prof. Asa Gray, of Cambridge.

Royal Institution of Great Britain.

WEEKLY EVENING MEETING,

Friday, May 25, 1883.

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Vice-President in the Chair.

PROFESSOR W. H. FLOWER, LL.D. F.R.S. P.Z.S. &c.

William Henry
Flower
On Whales, Past and Present, and their Probable Origin.

Few natural groups present so many remarkable, very obvious, and easily appreciated illustrations of several of the most important general laws which appear to have determined the structure of animal bodies, as those selected for my lecture this evening. We shall find the effects of the two opposing forces—that of heredity or conformation to ancestral characters, and that of adaptation to changed environment, whether brought about by the method of natural selection or otherwise—distinctly written in almost every part of their structure. Scarcely anywhere in the animal kingdom do we see so many cases of the persistence of rudimentary and apparently useless organs, those marvellous and suggestive phenomena which at one time seemed hopeless enigmas, causing despair to those who tried to unravel their meaning, looked upon as mere will-of-the-wisps, but now eagerly welcomed as beacons of true light, casting illuminating beams upon the dark and otherwise impenetrable paths through which the organism has travelled on its way to reach the goal of its present condition of existence.

It is chiefly to these rudimentary organs of the Cetacea and to what we may learn from them that I propose to call your attention. In each case the question may well be asked, granted that they are, as they appear to be, useless, or nearly so, to their present possessors, insignificant, imperfect, in fact *rudimentary*, as compared with the corresponding or homologous parts of other animals, are they survivals, remnants of a past condition, become useless owing to change of circumstances and environment, and undergoing the process of gradual degeneration, preparatory to their final removal from an organism to which they are only, in however small a degree, an incumbrance, or are they incipient structures, beginnings of what may in future become functional and important parts of the economy? These questions will call for an attempt at least at solution in each case as we proceed.

Before entering upon details, it will be necessary to give some general idea of the position, limits, and principal modifications of the group of animals from which the special illustrations will be drawn. The term "whale" is commonly but vaguely applied to all the larger

and middle-sized Cetacea, and though such smaller species as the dolphins and porpoises are not usually spoken of as whales, they may for all intents and purposes of zoological science be included in the term, and will come within the range of the present subject. Taken all together the *Cetacea* constitute a perfectly distinct and natural order of mammals, characterised by their purely aquatic mode of life and external fishlike form. The body is fusiform, passing anteriorly into the head without any distinct constriction or neck, and posteriorly tapering off gradually towards the extremity of the tail, which is provided with a pair of lateral pointed expansions of skin supported by dense fibrous tissue, called "flukes," forming together a horizontally-placed, triangular propelling organ. The fore-limbs are reduced to the condition of flattened ovoid paddles, incased in a continuous integument, showing no external sign of division into arm, forearm, and hand, or of separate digits, and without any trace of nails. There are no vestiges of hind-limbs visible externally. The general surface of the body is smooth and glistening, and devoid of hair. In nearly all species a compressed median dorsal fin is present. The nostrils open separately or by a single crescentic valvular aperture, not at the extremity of the snout, but near the vertex.

Animals of the order *Cetacea* abound in all known seas, and some species are inhabitants of the larger rivers of South America and Asia. Their organisation necessitates their life being passed entirely in the water, as on the land they are absolutely helpless; but they have to rise very frequently to the surface for the purpose of respiration. They are all predaceous, subsisting on living animal food of some kind. One genus alone (*Orca*) eats other warm-blooded animals, as seals and even members of its own order, both large and small. Some feed on fish, others on small floating crustacea, pteropods, and medusæ, while the staple food of many is constituted of the various species of Cephalopods, chiefly *Loligo* and other *Teuthidae*, which must abound in some seas in vast numbers, as they form almost the entire support of some of the largest members of the order. With some exceptions the Cetacea generally are timid, inoffensive animals, active in their movements, sociable and gregarious in their habits.

Among the existing members of the order there are two very distinct types—the Toothed Whales, or *Odontoceti*, and the Baleen Whales, or *Mystacoceti*, which present throughout their organisation most markedly distinct structural characters, and have in the existing state of nature no transitional forms. The extinct *Zeuglodon*, so far as its characters are known, does not fall into either of these groups as now constituted, but is in some respects intermediate, and in others more resembles the generalised mammalian type.

The important and interesting problem of the origin of the Cetacea and their relations to other forms of life is at present involved in the greatest obscurity. They present no more signs of affinity with any of the lower classes of vertebrated animals than do many of the members of their own class. Indeed, in all that essentially dis-

tinguishes a mammal from one of the oviparous vertebrates, whether in the osseous, nervous, vascular, or reproductive systems, they are as truly mammalian as any, even the highest, members of the class. Any supposed signs of inferiority are, as we shall see, simply modifications in adaptation to their peculiar mode of life. Similar modifications are met with in another quite distinct group of mammalia, the *Sirenia* (Dugongs and Manatees), and also, though in a less complete degree, in the aquatic Carnivora or seals. But these do not indicate any community of origin between these groups and the Cetacea. In fact, in the present state of our knowledge, the Cetacea are absolutely isolated, and little satisfactory reason has ever been given for deriving them from any one of the existing divisions of the class rather than from any other. The question has indeed often been mooted whether they have been derived from land mammals at all, or whether they may not be the survivors of a primitive aquatic form which was the ancestor not only of the whales, but of all the other members of the class. The materials for—I will not say solving—but for throwing some light upon this problem, must be sought for in two regions—in the structure of the existing members of the order, and in its past history, as revealed by the discovery of fossil remains. In the present state of science it is chiefly on the former that we have to rely, and this therefore will first occupy our attention.

One of the most obvious external characteristics by which the mammalia are distinguished from other classes of vertebrates is the more or less complete clothing of the surface by the peculiar modification of epidermic tissue called hair. The Cetacea alone appear to be exceptions to this generalisation. Their smooth, glistening exterior is, in the greater number of species, at all events in adult life, absolutely bare, though the want of a hairy covering is compensated for functionally by peculiar modifications of the structure of the skin itself, the epidermis being greatly thickened, and a remarkable layer of dense fat being closely incorporated with the tissue of the derm or true skin; modifications admirably adapted for retaining the warmth of the body, without any roughness of surface which might occasion friction and so interfere with perfect facility of gliding through the water. Close examination, however, shows that the mammalian character of hairiness is not entirely wanting in the Cetacea, although it is reduced to a most rudimentary and apparently functionless condition. Scattered, small, and generally delicate hairs have been detected in many species, both of the toothed and of the whalebone whales, but never in any situation but on the face, either in a row along the upper lip, around the blowholes or on the chin, apparently representing the large, stiff "vibrissæ" or "whiskers" found in corresponding situations in many land mammals. In some cases these seem to persist throughout the life of the animal; more often they are only found in the young or even the foetal state. In some species they have not been detected at any age.

Eschricht and Reinhardt counted in a new-born Greenland Right Whale (*Balaena mysticetus*) sixty-six hairs near the extremity of the upper jaw, and about fifty on each side of the lower lip, as well as a few around the blowholes, where they have also been seen in *Megaptera longimana* and *Balaenoptera rostrata*. In a large Rorqual (*Balaenoptera musculus*), quite adult and sixty-seven feet in length, stranded in Pevensey Bay in 1865, there were twenty-five white, straight, stiff hairs about half an inch in length, scattered somewhat irregularly on each side of the vertical ridge in which the chin terminated, extending over a space of nine inches in height and two and a half inches in breadth. The existence of these rudimentary hairs must have some significance beyond any possible utility they may be to the animal. Perhaps some better explanation may ultimately be found for them, but it must be admitted that they are extremely suggestive that we have here a case of heredity or conformation to a type of ancestor with a full hairy clothing, just on the point of yielding to complete adaptation to the conditions in which whales now dwell.

In the organs of the senses the Cetacea exhibit some remarkable adaptive modifications of structures essentially formed on the Mammalian type, and not on that characteristic of the truly aquatic Vertebrates, the fishes, which, if function were the only factor in the production of structure, they might be supposed to resemble.

The modifications of the organs of sight do not so much affect the eyeball as the accessory apparatus. To an animal whose surface is always bathed with fluid, the complex arrangement which mammals generally possess for keeping the surface of the transparent cornea moist and protected, the movable lids, the nictitating membrane, the lachrymal gland, and the arrangements for collecting and removing the superfluous tears when they have served their function cannot be needed, and hence we find these parts in a most rudimentary condition or altogether absent. In the same way the organ of hearing in its essential structure is entirely mammalian, having not only the sacculi and semicircular canals common to all but the lowest vertebrates, but the cochlea, and tympanic cavity with its ossicles and membrane, all, however, buried deep in the solid substance of the head; while the parts specially belonging to terrestrial mammals, those which collect the vibrations of the sound travelling through air, the pinna and the tube which conveys it to the sentient structures within are entirely or practically wanting. Of the pinna or external ear there is no trace. The meatus auditorius is certainly there, reduced to a minute aperture in the skin like a hole made by the prick of a pin, and leading to a tube so fine and long that it cannot be a passage for either air or water, and therefore can have no appreciable function in connection with the organ of hearing, and must be classed with the other numerous rudimentary structures that whales exhibit.

The organ of smell, when it exists, offers still more remarkable evidence of the origin of the Cetacea. In fishes this organ is specially

adapted for the perception of odorous substances permeating the water; the terminations of the olfactory nerves are spread over the inner plicated surface of a cavity near the front part of the nose, to which the fluid in which the animals swim has free access, although it is quite unconnected with the respiratory passages. Mammals, on the other hand, smell substances with which the atmosphere they breathe is impregnated; their olfactory nerve is distributed over the more or less complex foldings of the lining of a cavity placed more deeply in the head, but in immediate relation to the passages through which air is continually driven to and fro on its way to the lungs in respiration, and therefore in a most favourable position for receiving impressions from substances floating in that air. The whalebone whales have an organ of smell exactly on the mammalian type, but in a rudimentary condition. The perception of odorous substances diffused in the air, upon which many land mammals depend so much for obtaining their food, or for protection from danger, can be of little importance to them. In the more completely modified Odontocetes the olfactory apparatus, as well as that part of the brain specially related to the function of smell, is entirely wanting, but in both groups there is not the slightest trace of the specially aquatic olfactory organ of fishes. Its complete absence and the vestiges of the aërial organ of land mammals found in the *Mystacocetes* are the clearest possible indications of the origin of the Cetacea from air-breathing and air-smelling terrestrial mammalia. With their adaptation to an aquatic mode of existence, organs fitted only for smelling in air became useless, and so have dwindled or completely disappeared. Time and circumstances have not permitted the acquisition of anything analogous to the specially aquatic smelling apparatus of fishes, the result being that whales are practically deprived of whatever advantage this sense may be to other animals.

It is characteristic of the greater number of mammalia to have their jaws furnished with teeth having a definite structure and mode of development. In all the most typical forms these teeth are limited in number, not exceeding eleven on each side of each jaw, or forty-four in all, and are differentiated in shape in different parts of the series, being more simple in front, broader and more complex behind. Such a dentition is described as "heterodont." In most cases also there are two distinct sets of teeth during the lifetime of the animal, constituting a condition technically called "diphyodont."

All the Cetacea present some traces of teeth, which in structure and mode of development resemble those of mammals, and not those of the lower vertebrated classes, but they are always found in a more or less imperfect state. In the first place, at all events in existing species, they are never truly heterodont, all the teeth of the series resembling each other more or less or belonging to the condition called "homodont," and not obeying the usual numerical rule, often falling short of, but in many cases greatly exceeding it. The most typical Odontocetes, or toothed whales, have a large number of similar,

simple, conical, recurved, pointed teeth, alike on both sides and in the upper and under jaws, admirably adapted for catching slippery, living prey, such as fish, which are swallowed whole without mastication. In one genus (*Pontoporia*) there may be as many as sixty of such teeth on each side of each jaw, making 240 in all. The more usual number is from twenty to thirty. These teeth are never changed, being "monophyodont," and they are, moreover, less firmly implanted in the jaws than in land mammals, having never more than one root, which is set in an alveolar socket which is generally wide and loosely fitting, though perfectly sufficient for the simple purpose which the teeth have to serve.

Most singular modifications of this condition of dentition are met with in different genera of toothed whales, chiefly the result of suppression, sometimes of suppression of the greater number, combined with excessive development of a single pair. In one large group, the Ziphiods, although minute rudimentary teeth are occasionally found in young individuals, and sometimes throughout life, in both jaws, in the adults the upper teeth are usually entirely absent, and those of the lower jaw reduced to two, which may be very large and projecting like tusks from the mouth, as in *Mesoplodon*, or minute and entirely concealed beneath the gums, as in *Hyperoodon*,—an animal which is for all practical purposes toothless, yet in which a pair of perfectly formed though buried teeth remain throughout life, wonderful examples of the persistence of rudimentary and to all appearance absolutely useless organs. Among the *Delphinidae* similar cases are met with. In the genus *Grampus* the teeth are entirely absent in the upper, and few and early deciduous in the lower jaw. But the Narwhal exceeds all other Cetaceans, perhaps all other vertebrated animals, in the specialisation of its dentition. Besides some irregular rudimentary teeth found in the young state, the entire dentition is reduced to a single pair, which lie horizontally in the upper jaw, and both of which in the female remain permanently concealed within the bone, so that this sex is practically toothless, while in the male the right tooth usually remains similarly concealed and abortive, and the left is immensely developed, attaining a length equal to more than half that of the entire animal, projecting horizontally from the head in the form of a cylindrical or slightly tapering pointed tusk, with the surface marked by spiral grooves or ridges.

The meaning and utility of some of these strange modifications it is impossible, in the imperfect state of our knowledge of the habits of the Cetacea, to explain, but the fact that in almost every case a more full number of rudimentary teeth is present in early stages of existence, which either disappear, or remain as concealed and functionless organs, points to the present condition in the aberrant and specialised forms as being one derived from the more generalised type, in which the teeth were numerous and equal.

The *Mystacocetes*, or Whalebone Whales, are distinguished by entire absence of teeth, at all events after birth. But it is a remark-

able fact, first demonstrated by Geoffroy St. Hilaire, and since amply confirmed by Cuvier, Eschricht, Julin, and others, that in the foetal state they have numerous minute calcified teeth lying in the dental groove of both upper and lower jaws. These attain their fullest development about the middle of foetal life, after which period they are absorbed, no trace of them remaining at the time of birth. Their structure and mode of development has been shown to be exactly that characteristic of ordinary mammalian teeth, and it has also been observed that those at the posterior part of the series are larger, and have a bilobed form of crown, while those in front are simple and conical, a fact of considerable interest in connection with speculations as to the history of the group.

It is not until after the disappearance of these teeth that the baleen, or whalebone, makes its appearance. This remarkable structure, though, as will be presently shown, only a modification of a part existing in all mammals, is, in its specially developed condition as baleen, peculiar to one group of whales. It is therefore perfectly in accord with what might have been expected, that it is comparatively late in making its appearance. Characters that are common to a large number of species appear early, those that are special to a few, at a late period; alike both in the history of the race and of the individual.

Baleen consists of a series of flattened, horny plates, several hundred in number, on each side of the palate, separated by a bare interval along the middle line. They are placed transversely to the long axis of the palate, with very short spaces between them. Each plate or blade is somewhat triangular in form, with the base attached to the palate, and the apex hanging downwards. The outer edge of the blade is hard and smooth, but the inner edge and apex fray out into long, bristly fibres, so that the roof of the whale's mouth looks as if covered with hair, as described by Aristotle. The blades are longest near the middle of the series, and gradually diminish towards the front and back of the mouth. The horny plates grow from a dense fibrous and highly vascular matrix, which covers the palatal surface of the maxillæ, and which sends out lamellar processes, one of which penetrates the base of each blade. Moreover, the free edge of each of these processes is covered with very long vascular thread-like papillæ, one of which forms the central axis of each of the hair-like epidermic fibres of which the blade is mainly composed. A transverse section of fresh whalebone shows that it is made up of numbers of these soft vascular papillæ, circular in outline, each surrounded by concentrically arranged epidermic cells, the whole bound together by other epidermic cells, which constitute the smooth cortical (so-called "enamel") surface of the blade, and which, disintegrating at the free edge, allows the individual fibres to become loose and to assume the hair-like appearance spoken of before. These fibres differ from hairs in not being formed in depressed follicles in the enderon, but rather resemble those of which the horn of the rhinoceros is composed. The

blades are supported and bound together for a certain distance from their base, by a mass of less hardened epithelium, secreted by the surface of the palatal membrane or matrix of the whalebone in the intervals of the lamellar processes. This is the "intermediate substance" of Hunter, the "gum" of the whalers.

The function of the whalebone is to strain the water from the small marine mollusks, crustaceans, or fish upon which the whales subsist. In feeding they fill the immense mouth with water containing shoals of these small creatures, and then, on their closing the jaws and raising the tongue, so as to diminish the cavity of the mouth, the water streams out through the narrow intervals between the hairy fringe of the whalebone blades, and escapes through the lips, leaving the living prey to be swallowed. Almost all the other structures to which I am specially directing your attention, are, as I have mentioned, in a more or less rudimentary state in the Cetacea; the baleen, on the other hand, is an example of an exactly contrary condition, but an equally instructive one, as illustrating the mode in which nature works in producing the infinite variety we see in animal structures. Although appearing at first sight an entirely distinct and special formation, it evidently consists of nothing more than the highly modified papillæ of the lining membrane of the mouth, with an excessive and cornified epithelial development.

The bony palate of all mammals is covered with a closely adhering layer of fibrovascular tissue, the surface of which is protected by a coating of non-vascular epithelium, the former exactly corresponding to the derm or true skin, and the latter to the epiderm of the external surface of the body. Sometimes this membrane is perfectly smooth, but it is more often raised into ridges, which run in a direction transverse to the axis of the head, and are curved with the concavity backwards; the ridges moreover do not extend across the middle line, being interrupted by a median depression or *raphé*. Indications of these ridges are clearly seen in the human palate, but they attain their greatest development in the Ungulata. In oxen, and especially in the giraffe, they form distinct laminæ, and their free edges develop a row of pointed papillæ, giving them a pectinated appearance. Their epithelium is thick, hard, and white, though not horny. Although the interval between the structure of the ridges in the giraffe's palate and the most rudimentary form of baleen at present known is great, there is no difficulty in seeing that the latter is essentially a modification of the former, just as the hoof of the horse, with its basis of highly developed vascular laminæ and papillæ, and the resultant complex arrangement of the epidermic cells, is a modification of the simple nail or claw of other mammals, or as the horn of the rhinoceros is only a modification of the ordinary derm and epiderm covering the animal's body differentiated by a local exuberance of growth.

Though the early stages by which whalebone has been modified from more simple palate structures are entirely lost to our sight, probably for ever, the conditions in which it now exists in different

species of whales, show very marked varieties of progress, from a simple comparatively rudimental and imperfect condition, to what is perhaps the most wonderful example of mechanical adaptation to purpose known in any organic structure. These variations are worth dwelling upon for a few minutes, as they illustrate in an excellent manner the gradual modifications that may take place in an organ, evidently in adaptation to particular requirements, the causation of which can be perfectly explained upon Darwin's principle of natural selection.

In the Rorquals or fin-whales (genus *Balaenoptera*), found in almost all seas, and so well known off our own coasts, the largest blades in an animal 70 feet long do not exceed 2 feet in length, including their hairy terminations; they are in most species of a pale horn colour, and their structure is coarse and inelastic, separating into thick, stiff fibres, so that they are of no value for the ordinary purposes to which whalebone is applied to the arts. These animals feed on fish of considerable size, from herrings up to cod, and for foraging among shoals of these creatures the construction of their mouth and the structure of their baleen is evidently sufficient. This is the type of the earliest known extinct forms of whales, and it has continued to exist, with several slight modifications, to this day, because it has fulfilled one purpose in the economy of nature. Other purposes for which it was not sufficient have been supplied by gradual changes taking place, some of the stages of which are seen in the intermediate conditions still exhibited in the Megaptera, and in the Atlantic and Southern Right Whales. Before describing the extreme modifications in the direction of complexity, I may mention, to show the range at present presented in the development of baleen, that there has lately been discovered in the North Pacific a species called by the whalers the Californian Grey Whale (*Rachianectes glaucus*), which shows the opposite extreme of simplicity. The animal is from 30 to 40 feet in length; the baleen blades are only 182 on each side (according to Scammon) and far apart, very short (the longest being from 14 to 16 inches in length), light brown or nearly white in colour, and still more coarse in grain and inelastic than that of the Rorquals. The food of these whales is not yet known with certainty. They have been seen apparently seeking for it along soft bottoms of the sea, and fuci and mussels have been found in their stomachs.

In the Greenland Right Whale of the circumpolar seas, the Bowhead of the American whalers (*Balaena mysticetus*), all the peculiarities which distinguish the head and mouth of the whales from other mammals have attained their greatest development. The head is of enormous size, exceeding one-third of the whole length of the creature. The cavity of the mouth is actually larger than that of the body, thorax, and abdomen together. The upper jaw is very narrow, but greatly arched from before backwards, to increase the height of the cavity and allow for the great length of the baleen, the enormous rami of the mandibles are widely separated posteriorly, and have a

still further outward sweep before they meet at the symphysis in front, giving the floor of the mouth the shape of an immense spoon. The baleen blades attain the number of 350 or more on each side, and those in the middle of the series have a length of ten or even twelve feet. They are black in colour, fine and highly elastic in texture, and fray out at the inner edge and ends into long, delicate, soft, almost silky, but very tough hairs.

How these immensely long blades depending vertically from the palate were packed into a mouth the height of which was scarcely more than half their length, was a mystery not solved until a few years ago. Captain David Gray, of Peterhead, at my request, first gave us a clear idea of the arrangement of the baleen in the Greenland whale, and showed that the purpose of its wonderful elasticity was not primarily at least the benefit of the corset and umbrella makers, but that it was essential for the correct performance of its functions. It may here be mentioned that the modification of the mouth structure of the Right Whale is entirely in relation to the nature of its food. It is by this apparatus that it is enabled to avail itself of the minute but highly nutritious crustaceans and pteropods which swarm in immense shoals in the seas it frequents. The large mouth enables it to take in at one time a sufficient quantity of water filled with these small organisms, and the length and delicate structure of the baleen provides an efficient strainer or hair sieve by which the water can be drained off. If the baleen were, as in the Rorquals, short and rigid, and only of the length of the aperture between the upper and lower jaws when the mouth was shut, when the jaws were separated a space would be left beneath it through which the water and the minute particles of food would escape together. But instead of this, the long, slender, brush-like ends of the whalebone blades, when the mouth is closed, fold back, the front ones passing below the hinder ones in a channel lying between the tongue and the bone of the lower jaw. When the mouth is opened their elasticity causes them to straighten out like a bow that is unbent, so that at whatever distance the jaws are separated, the strainer remains in perfect action, filling the whole of the interval. The mechanical perfection of the arrangement is completed by the great development of the lower lip, which rises stiffly above the jaw-bone, and prevents the long, slender, flexible ends of the baleen being carried outwards by the rush of water from the mouth, when its cavity is being diminished by the closure of the jaws and raising of the tongue. The interest and admiration excited by the contemplation of such a beautifully adjusted piece of mechanism is certainly heightened by the knowledge that it has been brought about by the gradual adaptation and perfection of structures common to the whole class of animals to which the whale belongs.

Few points of the structure of whales offer so great a departure from the ordinary mammalian type as the limbs. The fore-limbs are reduced to the condition of simple paddles or oars, variously shaped, but always flattened and more or less oval in outline. They are

freely movable at the shoulder-joint, where the humerus or upper-arm bone articulates with the shoulder-blade in the usual manner, but beyond this point, except a slight flexibility and elasticity, there is no motion between the different segments. The bones are all there, corresponding in number and general relations with those of the human or any other mammalian arm, but they are flattened out, and their contiguous ends, instead of presenting hinge-like joints, come in contact by flat surfaces, united together by strong ligamentous bands, and all wrapped up in an undivided covering of skin, which allows externally of no sign of the separate and many-jointed fingers seen in the skeleton.

Up to the year 1865 it was generally thought that there was nothing to be found between this bony framework and the covering skin, with its inner layer of blubber, except dense fibrous tissue, with blood-vessels and nerves sufficient to maintain its vitality. Dissecting a large Rorqual, 67 feet in length, upon the beach of Pevensey Bay in that year, I was surprised to find lying upon the bones of the fore-arm well-developed muscles, the red fibres of which reached nearly to the lower end of these bones, ending in strong tendons, passing to, and radiating out on, the palmar surface of the hand. Circumstances then prevented me following out the details of their arrangement and distribution, but not long afterwards Professor Struthers, of Aberdeen, had an opportunity of carefully dissecting the fore-limb of another whale of the same species, and he has recorded and figured his observations in the 'Journal of Anatomy' for November 1871. He found on the internal or palmar aspect of the limb three distinct muscles corresponding in attachments to the flexor carpi ulnaris, the flexor profundus digitorum, and the flexor longus pollicis of man, and on the opposite side but one, the extensor communis digitorum.* Large as these muscles actually are, yet, compared with the size of the animal, they cannot but be regarded as rudimentary, and being attached to bones without regular joints and firmly held together by unyielding tissues, their functions must be reduced almost to nothing. But rudimentary as the muscles of the Fin-whales are, lower stages of degradation of the same structures are found in other members of the group. In some they are indeed present in form, but their muscular structure is gone, and they are reduced in most of the toothed whales to mere fibrous bands, scarcely distinguishable from the surrounding tissue which connects the inner surface of the skin with the bone. It is impossible to contemplate these structures without having the conviction forced home that here are the remains of parts once of use to their possessor, now, owing to the complete change of purpose and mode of action of the limb, reduced to a condition of atrophy verging on complete disappearance.

The changes that have taken place in the hind-limbs are even

* The muscles of the fore-arm of an allied species, *Balaenoptera rostrata*, were described by Macalister in 1868, and Perrin in 1870.

more remarkable. In all known Cetacea (unless *Platanista* be really an exception) a pair of slender bones are found suspended a short distance below the vertebral column, but not attached to it, about the part where the body and the tail join. In museum skeletons these bones are often not seen, as, unless special care has been taken in the preparation, they are apt to get lost. They are, however, of much importance and interest, as their relations to surrounding parts show that they are the rudimentary representatives of the pelvic or hip bones, which in other mammals play such an important part in connecting the hind-limbs with the rest of the skeleton. The pelvic arch is thus almost universally present, but of the limb proper there is, as far as is yet known, not a vestige in any of the large group of toothed whales, not even in the great Cachalot or Sperm Whale, although it should be mentioned that it has never been looked for in that animal with any sort of care. With the Whalebone Whales, however, at least to some of the species, the case is different. In these animals there are found, attached to the outer and lower side of the pelvic bone, other elements, bony or only cartilaginous as the case may be, clearly representing rudiments of the first and in some cases the second segment of the limb, the thigh or femur, and the leg or tibia. In the small *Balaenoptera rostrata* a few thin fragments of cartilage, imbedded in fibrous tissue attached to the side of the pelvic bone, constitute the most rudimentary possible condition of a hind-limb, and could not be recognised as such but for their analogy with other allied cases. In the large Rorqual, *Balaenoptera musculus*, 67 feet long, previously spoken of, I was fortunate enough in 1865 to find attached by fibrous tissue to the side of the pelvic bone (which was sixteen inches in length) a distinct femur, consisting of a nodule of cartilage of a slightly compressed, irregularly oval form, and not quite one inch and a half in length. Other specimens of the same animal dissected by Van Beneden and Professor Struthers have shown the same; in one case, partial ossification had taken place. In the genus *Megaptera* a similar femur has been described by Eschricht; and the observations of Reinhardt have shown that the Greenland Right Whale (*Balaena mysticetus*) has not only a representative of the femur developed far more completely than in the Rorqual, being from six to eight inches in length and completely ossified, but also a second smaller and more irregularly formed bone, representing the tibia. Our knowledge of these parts in this species has recently been greatly extended by the researches of Dr. Struthers, who has published in the 'Journal of Anatomy' for 1881 a most careful and detailed account of the dissection of several specimens, showing the amount of variation to which these bones (as with most rudimentary structures) are liable in different individuals, and describing for the first time their distinct articulation one with the other by synovial joints and capsular ligaments, and also the most remarkable and unlooked-for presence of muscles passing from one bone to the other, representing the adductors and flexors of mammals with completely

developed limbs, but so situated that it is almost impossible to conceive that they can be of any use; the whole limb, such as it is, being buried deep below the surface, where any movement, except of the most limited kind, must be impossible. Indeed, that the movement is very limited and of no particular importance to the animal was shown by the fact that in two out of eleven whales dissected the hip-joint was firmly ankylosed (or fixed by bony union) though without any trace of disease. In the words of Dr. Struthers, "Nothing can be imagined more useless to the animal than rudiments of hind-legs entirely buried beneath the skin of a whale, so that one is inclined to suspect that these structures must admit of some other interpretation. Yet, approaching the inquiry with the most sceptical determination, one cannot help being convinced, as the dissection goes on, that these rudiments really are femur and tibia. The functional point of view fails to account for their presence. Altogether they present for contemplation a most interesting instance of those significant parts, rudimentary structures."

We have here a case in which it is not difficult to answer the question before alluded to, often asked with regard to rudimentary parts, are they disappearing or are they incipient organs? We can have no hesitation in saying that they are the former. All we know of the origin of limbs shows that they commence as outgrowths upon the surface of the body, and that the first-formed portions are the most distal segments. The limb, as proved by its permanent state in the lowest Vertebrates, and by its embryological condition in higher forms, is at first a mere projection or outward fold of the skin, which, in the course of development, as it becomes of use in moving or supporting the animal, acquires the internal framework which strengthens it and perfects its functions. It would be impossible on any theory of causation yet known, to conceive of a limb gradually developed from within outwards. On the other hand, its disappearance would naturally take place in the opposite direction; projecting parts which had become useless, being in the way, would, like all the other prominences on the surface of the whales, hair, ears, &c., be removed, while the most internal, offering far less interference with successful carrying on the purposes of life, would be the last to disappear, lingering, as in the case of the Greenland Whale, long enough to reveal their wonderful history to the anatomist who has been fortunate enough to possess the skill and the insight to interpret it.

Time will not allow of more illustrations drawn from the structure of existing Cetacea; we turn next to what the researches of palæontology teach of the past history of the order. Unfortunately this does not at present amount to very much. As is the case with nearly all other orders of mammals, we know nothing of their condition, if they existed, in the mesozoic age. Even in the Cretaceous seas, the deposits at the bottom of which are so well adapted to preserve the remains of the creatures which swam in them, not a fragment of any whale or whale-like animal has been found. The earliest Cetaceans

of whose organisation we have any good evidence, are the *Zeuglodon*s of the Eocene formations of North America. These were creatures whose structure, as far as we know it, was intermediate between that of the existing suborders of whales, having the elongated nasal bones and anterior position of the nostrils of the *Mystacocetes*, with the teeth of the *Odontocetes*, and with some characters more like those of the generalised mammalian type, than of any of the existing forms. In fact *Zeuglodon* is precisely what we might have expected *a priori* an ancestral form of whale to have been. The remarkable smallness of its cerebral cavity, compared with the jaws and the rest of the skull, so different from that of modern Cetaceans, is exactly paralleled in the primitive types of other groups of mammals. The teeth are markedly differentiated in different parts of the series. In the anterior part of both jaws they are simple, conical, or slightly compressed and sharp pointed. The first three of the upper jaw are distinctly implanted in the premaxillary bone, and so may be reckoned as incisors. The tooth which succeeds, or the canine, is also simple and conical, but it does not greatly exceed the others in size. This is followed by five teeth with two distinct roots and compressed pointed crowns, with denticulated cutting edges. It has been thought that there was evidence of a vertical succession of the molar teeth, as in diphyodont mammals, but the proof of this is not quite satisfactory. Unfortunately the structure of the limbs is most imperfectly known. A mutilated humerus has given rise to many conjectures; to some anatomists it appears to indicate freedom of motion at the elbow-joint, while to others its characters seem to be those of the ordinary Cetacea. Of the structure of the pelvis and hind-limb we are at present in ignorance.

From the middle Miocene period fossil Cetacea are abundant, and distinctly divided into the two groups now existing. The *Mystacocetes*, or Whalebone Whales, of the Miocene seas were, as far as we know now, only *Balaenopterae*, some of which (as the genus *Cetotherium*) were, in the elongated flattened form of the nasal bones, the greater distance between the occipital and frontal bones at the top of the head, and the greater length of the cervical vertebrae, more generalised than any now existing. In the shape of the mandible also, Van Beneden, to whose researches we are chiefly indebted for a knowledge of these forms, discerns some approximation to the *Odontocetes*. Right Whales (*Balaena*) have not been found earlier than the Pliocene period, and it is interesting to note that instead of the individuals diminishing in bulk as we approach the times we live in, as with many other groups of animals, the contrary has been the case, no known extinct species of whales equalling in size those that are now to be met with in the ocean. The size of whales, as of all other things whose most striking attribute is magnitude, has been greatly exaggerated; but when reduced to the limits of sober fact, the Greenland Right Whale of 50 feet long, the Sperm Whale of 60, and the Great Northern Rorqual (*Balaenoptera Sibbaldii*) of 80, exceed all

other organic structures known, past or present. Instead of living in an age of degeneracy of physical growth, we are in an age of giants, but it may be at the end of that age. For countless centuries impulses from within and the forces of circumstances from without have been gradually shaping the whales into their present wonderful form and gigantic size, but the very perfection of their structure and their magnitude combined, the rich supply of oil protecting their internal parts from cold, the beautiful apparatus of whalebone by which their nutrition is provided for, have been fatal gifts, which, under the sudden revolution produced on the surface of the globe by the development of the wants and arts of civilised man, cannot but lead in a few years to their extinction.

It does not need much foresight to divine the future history of whales, but let us return to the question with which we started, What was their probable origin?

In the first place, the evidence is absolutely conclusive that they were not originally aquatic in habit, but are derived from terrestrial mammals of fairly high organisation, belonging to the placental division of the class,—animals in which a hairy covering was developed, and with sense organs, especially that of smell, adapted for living on land; animals, moreover, with four completely-developed pairs of limbs on the type of the higher vertebrata, and not of that of fishes. Although their teeth are now of the simple homodont and diphyodont type, there is much evidence to show that this has taken place by the process of degradation from a more perfect type, even the foetal teeth of whalebone whales showing signs of differentiation into molars and incisors, and many extinct forms, not only the Zeuglodons, but also true dolphins, as the Squalodons, having a distinct heterodont dentition, the loss of which, though technically called a "degradation," has been a change in conformity to the habits and needs of the individuals. So much may be considered very nearly, if not quite, within the range of demonstrated facts, but it is in determining the particular group of mammals from which the Cetacea arose that greater difficulties are met with.

One of the methods by which a land mammal may have been changed into an aquatic one is clearly shown in the stages which still survive among the Carnivora. The seals are obviously modifications of the land Carnivora, the Otariæ, or sea-lions and sea-bears, being curiously intermediate. Many naturalists have been tempted to think that the whales represent a still further stage of the same kind of modification. So firmly has this idea taken root that in most popular works on zoology in which an attempt has been made to trace the pedigree of existing mammals, the Cetacea are definitely placed as offshoots of the Pinnipedia, which in their turn are derived from the Carnivora. But there is to my mind a fatal objection to this view. The seal of course has much in common with the whale, inasmuch as it is a mammal adapted for an aquatic life, but it has been converted to its general fish-like form by the peculiar development of its

hind-limbs into instruments of propulsion through the water; for though the thighs and legs are small, the feet are large and are the special organs of locomotion, the tail being quite rudimentary. The two feet applied together form an organ very like the tail of a fish or whale, and functionally representing it, but only functionally, for the time has I trust quite gone by when the Cetacea were defined as animals with the "hinder limbs united, forming a forked horizontal tail." In the whales, as we have seen, the hind-limbs are aborted and the tail developed into a powerful swimming organ. Now it is very difficult to suppose that when the hind-limbs had once become so well adapted to a function so essential to the welfare of the animal as that of swimming, they could ever have become reduced and their action transferred to the tail;—the animal must have been in a too helpless condition to maintain its existence during the transference, if it took place, as we must believe, gradually. It is far more reasonable to suppose that whales were derived from animals with large tails, which were used in swimming, eventually with such effect that the hind-limbs became no longer necessary, and so gradually disappeared. The powerful tail, with lateral cutaneous flanges, of an American species of otter (*Pteronura sandbachii*) or the still more familiar tail of the beaver, may give some idea of this member in the primitive *Cetacea*. I think that this consideration disposes of the principal argument in favour of the whales being related to the seals, as most of the other resemblances, such as those in the characters of their teeth, are evidently resemblances of analogy related to similarity of habit.

As pointed out long ago by Hunter, there are numerous points in the structure of the visceral organ of the Cetacea far more resembling those of the Ungulata than the Carnivora. These are the complex stomach, simple liver, respiratory organs, and especially the reproductive organs and structures relating to the development of the young. Even the skull of *Zeuglodon*, which has been cited as presenting a great resemblance to that of a seal, has quite as much likeness to one of the primitive pig-like Ungulates, except in the purely adaptive character of the form of the teeth.

Though there is, perhaps, generally more error than truth in popular ideas on natural history, I cannot help thinking that some insight has been shown in the common names attached to one of the most familiar of Cetaceans by those whose opportunities of knowing its nature have been greatest—"Sea-Hog," "Sea-Pig," or "Herring-Hog" of our fishermen, *Meerschwein* of the Germans, corrupted into the French "Marsouin," and also "Porcpoisson," shortened into "Porpoise."

The difficulty that might be suggested in the derivation of the Cetacea from the Ungulata, arising from the latter being at the present day mainly vegetable feeders, is not great, as the primitive Ungulates were probably omnivorous, as their least modified descendants, the pigs, are still; and the aquatic branch might easily have

gradually become more and more piscivorous, as we know from the structure of their bones and teeth, the purely terrestrial members have become by degrees more exclusively graminivorous.

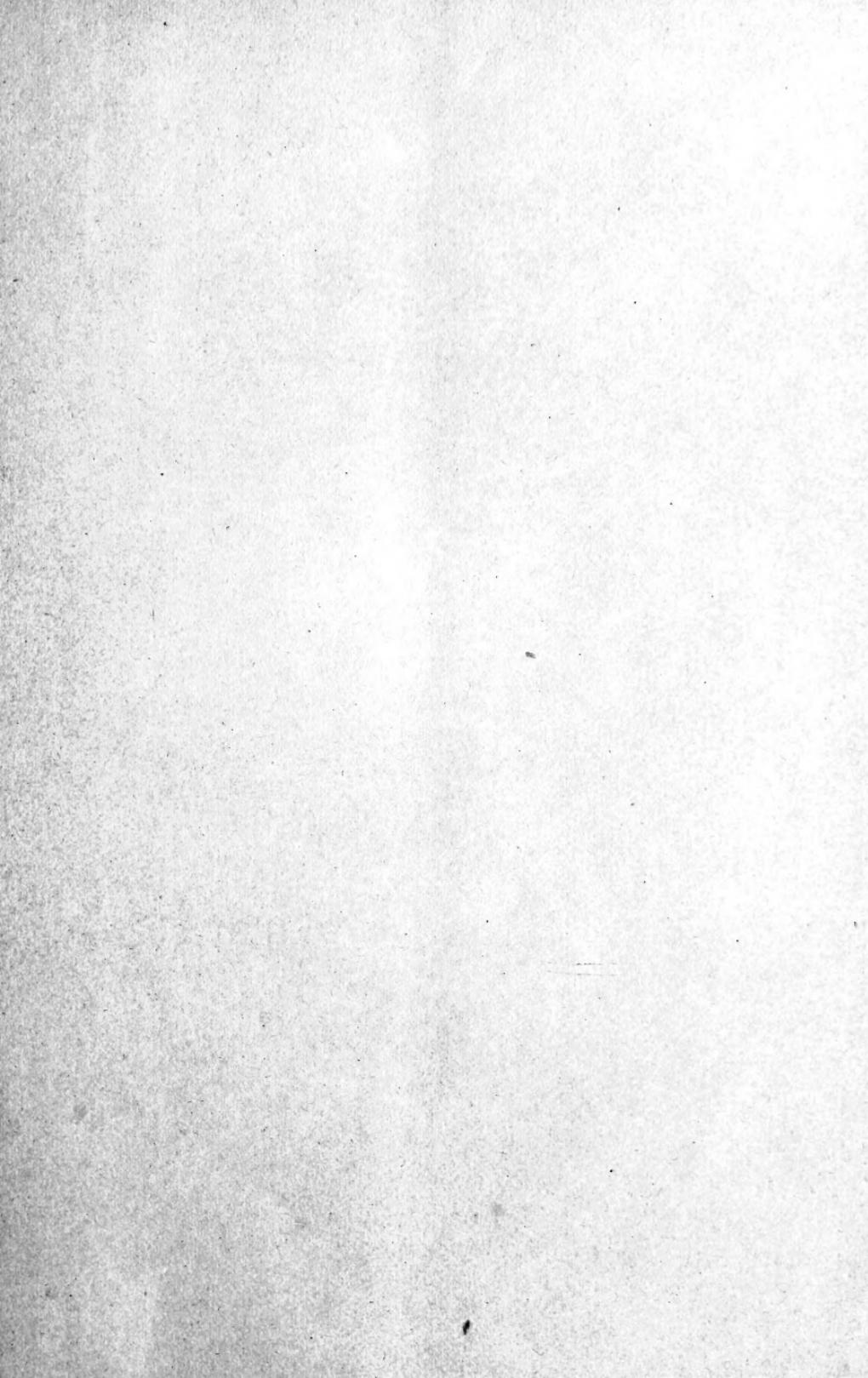
One other consideration may remove some of the difficulties that may arise in contemplating the transition of land mammals into whales. The Gangetic Dolphin (*Platanista*) and the somewhat related *Inia* of South America, which retain several rather generalised mammalian characters, and are related to some of the earliest known European Miocene dolphins, are both to the present day exclusively fluviatile, being found in the rivers they inhabit almost up to their very sources, more than a thousand miles from the sea. May this not point to the freshwater origin of the whole group, and thus account for their otherwise inexplicable absence from the Cretaceous seas?

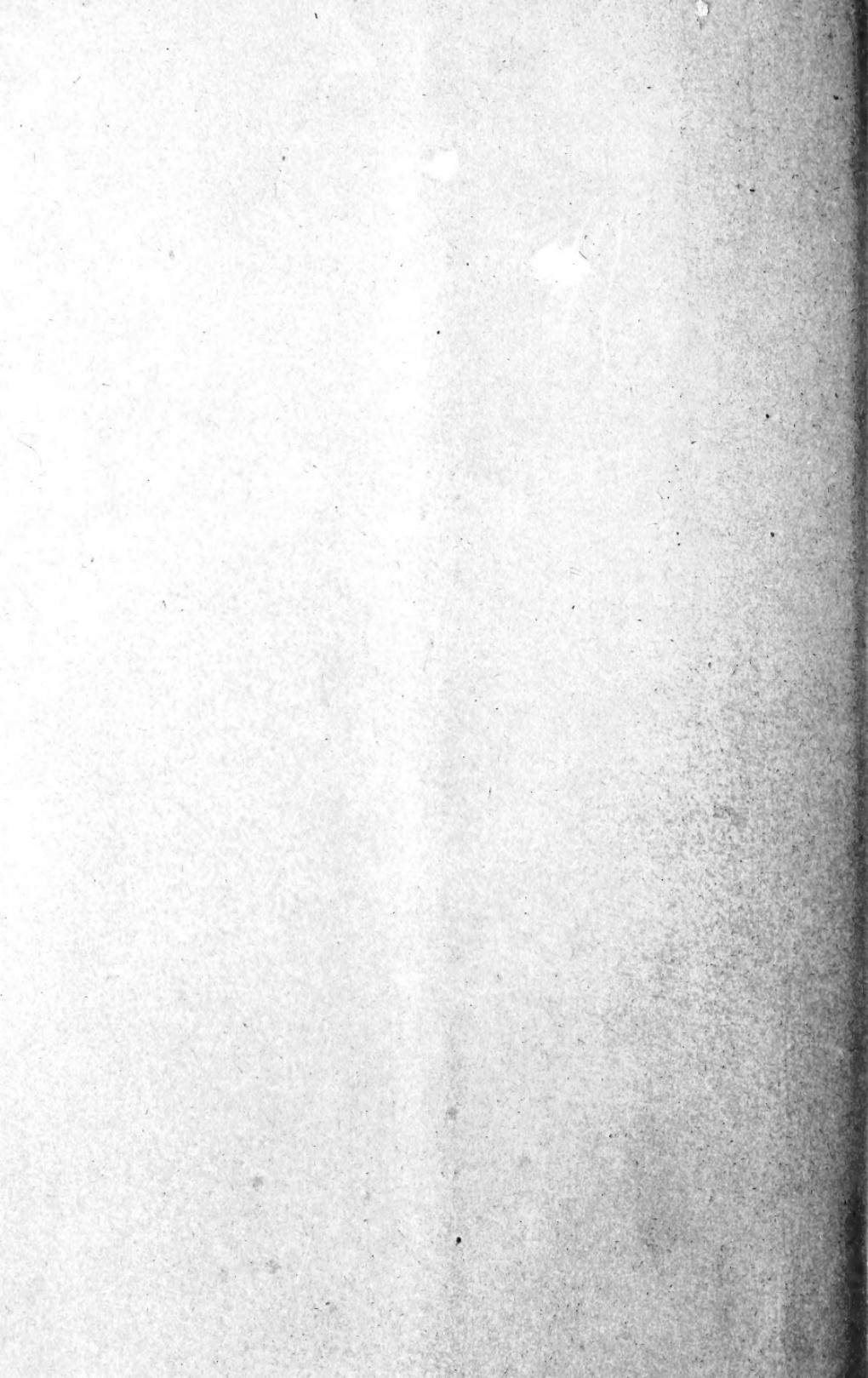
We may conclude by picturing to ourselves some primitive generalised, marsh-haunting animals with scanty covering of hair like the modern hippopotamus, but with broad, swimming tails and short limbs, omnivorous in their mode of feeding, probably combining water-plants with mussels, worms, and freshwater crustaceans, gradually becoming more and more adapted to fill the void place ready for them on the aquatic side of the borderland on which they dwelt, and so by degrees being modified into dolphin-like creatures inhabiting lakes and rivers, and ultimately finding their way into the ocean. Here the disappearance of the huge Enaliosaurians, the *Ichthyosauri* and *Plesiosauri*, which formerly played the part the Cetacea do now, had left them ample scope. Favoured by various conditions of temperature and climate, wealth of food supply, almost complete immunity from deadly enemies, and illimitable expanses in which to roam, they have undergone the various modifications to which the Cetacean type has now arrived, and gradually attained that colossal magnitude which we have seen was not always an attribute of the animals of this group.

Please to recollect, however, that this is a mere speculation, which may or may not be confirmed by subsequent palaeontological discovery. Such speculations are, I trust, not without their use and interest, especially when it is distinctly understood that they are offered only as speculations and not as demonstrated facts.

[W. H. F.]









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